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# THE WILLIAMSONIAS OF THE MIXTECA ALTA

G. R. WIELAND

(WITH TEN FIGURES)

The great plateau and mountain region in the central and western portion of the southern Mexican state of Oaxaca is commonly known in Mexico as the Mixteca alta, or high country of the Mixteca Indians. This name is used in contradistinction to the Mixteca baja, or portions of the lower country or tierra caliente over which the Mixtecas have extended. Simply speaking, then, the Mixteca alta is a portion of the southern edge of the Cordilleran system facing the Pacific and extending through western Oaxaca to the border of Guerrero, or into the latter state. Here, during some five months of the past winter and spring I have had the pleasure of continuing field work on the American fossil cycads under the auspices of the Instituto Geologico Nacional de Mexico. I have the kind permission of the director, Señor AGUILÉRA, to note in this preliminary manner that the results obtained are regarded as of the greatest interest to paleobotanists.

The field work has included the making of an accurate section through fully 2000 feet of plant beds of Rhät-Liassic age, full of cycads in as great a variety of types as has thus far been encountered anywhere in the world. Indeed, considering the fine material obtained from the localities noted in the valley of the Rio Nochixtlan near Tlaxiaco, at Mixtepec on the Rio Tlaxiaco, notably all around the Mina Consuelo, about El Cerro del Lucero, and the Rosario region to the southwest of Tezoatlan, as well as elsewhere, and considering, moreover, the almost endless opportunity for opening up quarries in all this extensive country, I am of the opinion that the Mixteca alta is one of the most promising and accessible regions for the student of fossil plants yet discovered.

True enough, these localities are distant from the railway 50 to 150 miles or more, over the roughest of mountain trails. And as mountain succeeds mountain with scarce a valley between, there are some real difficulties for the collector, who must send out his material in blocks of limited size, such as can be loaded on the backs of the tough little burros, or on the strongest mules, which can carry a pair of boxes of 200 pounds weight each. Hence, it more than once becomes necessary to break the splendid slabs all covered with leaf impressions, and often bearing flowers, which one can secure in even the smaller quarries almost without limit.

But for a country so distant, there are many very distinct advantages and no final obstacles. Animals are trusty; the Indians are good and cheap workmen; one is everywhere met with great courtesy; it is a source of much interest to find the high degree of comfort to be had in some of the most distant of the towns and villages; the food is always good, and even in the far mountains one can always get eggs and tortillas. All in all, if one is only fairly fore-wise, to spend a winter in the sunshine, the forests, and amidst the grand scenery of the Mixteca alta is much more like enjoying oneself in some geological sanatorium, as it were, than like hard work. For the naturalist ever finds a thousand and one points of interest, and soon becomes accustomed to ride 20 to 50 miles a day as he may need; while if interested in the cycads he can find places farther down the cañons and deep valleys where species of Dioon are fruiting hard by strata yielding the fossil forms in profusion.

The great thickness of these Oaxacan plant beds has been noted; but as to their exact age I am not sure, it being as yet early to form a fair conclusion. Glossopteris, rather than merely the sagenopterids, is considered present; and there is also a wealth of taeniopterids of older type, as well as a fine series of stems of a small but distinct lepidodendrid, and many leaves of *Noeggerathiopsis Hislopi* Bunbury. But otherwise the facies is uppermost Triassic, if indeed Liassic genera may not in the end be found to preponderate. A similarity to the Gondwanas of India suggests itself.

But what commands our attention at present, far beyond the precise age of these beds, is the fact that there abound in them in great variety the imprints, casts, and molds of many fruits of Williamsonia, closely associated with Zamites, Otozamites, Podozamites, Pterozamites, Ptilophyllum, and Dictyozamites, fronds as well as seeds. One of the strobili is a mold of just such an ovulate fruit as BUCKLAND figured under the name of Podocarya in the *Bridgewater treatises*, the original of which should be at Oxford, but could not be found when a search was made for it a few years since, as Professor SEWARD of Cambridge has informed me. Also, there is a considerable number of the large buds inclosed by heavy ramentum-covered bracts of the same size and appearance as those from the Yorkshire coast. One favorable circumstance that has conduced to frequent preservation of the surface characters of the ovulate fruits is the formation by the outer zone of a layer of coal, which while liable to checking affords an excellent indicator for which one may keep constant watch. Furthermore, the close association of these fruits, leaves, and stems, though the latter are not well preserved as a rule, leads to the hope that as the collections come to embrace a wider range of localities, and the data of association come to be better known, more than one restoration of the complete plant can be made. That silicified forms may yet be found is proven by the occurrence of a well-silicified log of a new species of Araucarioxylon.

Especially interesting is the occurrence at Mixtepec on the Rio Tlaxiaco of fruits of small size borne on slender stems, and also those with broad bladelike bracts of thin texture, if they are not indeed sepals or petals. These small fruits, while not preserved in finer details, are abundant, and are quite uniformly accompanied by small, much-branched stems, and by numerous fronds no more than $10^{cm}$ in length; though these may have been bipinnate.

Of primary importance is a single fairly well-preserved impression of a staminate disk from midway up in the plant beds in the main barranca between El Cerro del Venado on the south and El Cerro del Lucero on the north, near the coal outcrops of Mina Consuelo, 15 miles from Tezoatlan. On my return from the Mixteca alta I supposed that I had not found any of the staminate organs of the cycadophytes; although various interesting fruits of seed ferns appeared to be present. But I found on my desk at the Instituto Geologico a letter from Professor NATHORST, dated from England and telling me that he had just visited the Yorkshire coast, where he had succeeded in finding the first definitely recognizable male flowers of Williamsonia, these agreeing essentially with the flower of Cycadeoidea as first discovered in the type of *C. ingens* and described in my *Studies of American fossil cycads*, parts I–IV.

It can be readily understood that I had kept a sharp watch for such disks during all the field work, and that after reading Professor NATHORST'S letter this watch was made closer still while the various specimens were being unpacked, placed in order, and further developed. But not until all this work had been done did I finally, in an idle moment, uncover a staminate disk on a slab from near Mina Consuelo. Then I recognized that a form I had suspected at one time was a disk had been truly such, though poorly preserved. It seems I had not chanced on quite the best disk locality. Better localities will yet be found.

The El Consuelo Williamsonia staminate disk is a reduced campanulate form of the size and general structure indicated in *fig. 2*. As there shown, however, the number of fronds is arbitrarily taken for purposes of interpretation as five, instead of the true number of eight or ten. One cannot be quite sure of the exact number in the specimen. The important structural feature, however, is that instead of a bipinnate frond as in Cycadeoidea,[1] there is a small strictly once-pinnate form, the rachises bearing only two lateral rows of synangia. These, however, are still of the marattiaceous or cycadeoidean size and structure. The component fronds project beyond the disk only to a height of about $1.5^{\mathrm{cm}}$. The basal region appears to be rather thin in texture; but the state of preservation as well as the association with other fruits and leaves all go to indicate that these disks and doubtless those of other species and genera should yet be found in abundance.

There can be no gainsaying the supreme importance of this fossil flower in enabling us to form more exact and adequate conceptions of the course of evolution leading up to and resulting in the present diversity of gamopetalous plants. In describing the flowers of *Cycadeoidea ingens* and *C. dacotensis*, I pointed out that the disk type of cycadophytean flower clearly indicated previous stages with the staminate organs spirally inserted beneath an apical cone or series of likewise spirally inserted megasporophylls, and that readily conceivable reductions and changes in such a primitively organized inflorescence or fertile apex or branch fully indicated the mode of origin of Liriodendron. Whence it followed that the Magnoliaceae must be among if not the most primitive of all the angiosperms. In this I believe I was clearly the first; though HALLIER soon independently reached similar conclusions as to the origin of the Magnoliaceae, and likewise cited Liriodendron.

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[1] I followed the old usage of calling these fronds pinnate in my descriptions; but ARBER has called them bipinnate forms. It seems rather more correct so to do.

Later, ARBER and PARKIN visualized in the *Annals of botany* the conception of a primitive semi-cycadean angiosperm ancestor with its crown of reduced, once-pinnate, spirally inserted microsporophylls surmounted by similarly set carpophylls; and these authors at the same time carried much further the idea that the true mode of angiosperm evolution, so long completely hidden, was at last indicated in all its broader outlines by reasonably direct evidence.

In ARBER and PARKIN'S ancestral stage we certainly behold a very primitive and decidedly plastic type, which they choose to call a hemiangiosperm, though I perversely prefer to group such plants under SAPORTA'S old term of proangiosperm.[2] It is one of the hypothetical forms, moreover, which is not only so readily conceivable as undergoing an infinity of modifications in the direction of higher forms, but one which, as I have long since told ARBER, we may confidently expect will yet be found in the fossil stage.

Despite all this progress, the actual mode of modification leading into the more complex types of angiospermous flowers has remained obscure. While SCOTT, especially, as well as HALLIER, ARBER and PARKIN, BESSEY, and others, as well as myself, have all insistently urged that the path has thus really been blazed to a knowledge of the evolution of the angiosperm groups, no one has yet been in a position to bring the final methods more clearly into view. Now, however, I believe we can do so in the case of all but the extremely modified families, if not indeed ultimately in these too, by means of analogic methods combined with comparative morphology.

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[2] From a long letter that ARBER has been kind enough to write me, I know his views on the question of whether in hypothesizing the more immediate angiosperm ancestors we may use the old term proangiosperms, or must define a new and different group, the "hemiangiosperms," as he has proposed. I duly respect these views and think it is of importance that they receive a more thorough consideration than can be accorded them here.

At the same time, I wish to point out that we should duly honor SAPORTA as one of the pioneers, who, whether clearly or not, glimpsed an important truth when he placed Williamsonia among his proangiosperms. To claim that the proangiosperms of SAPORTA, as a great and more or less hypothetical group, either had to be, or in his day could have been delimited would to my mind be both impractical and unjust. Moreover, the important point is that we may well allow that SAPORTA was taking a glance backward in the direction of primitive forms even more than forward. Indeed, it is both fair and convenient to remember that the proangiosperms, as a great group leading into the angiosperms, could have their gymnosperm section, and yet logically include other truly lineal families, these being of hardly more than family distance from the Cycadeoideae at best. For these reasons, partly pertinent at least it seems to me that to use fairly the term hemiangiosperm we must go much farther back, to where by another hiatus the proangiosperms merge into the more primitive fern derivatives.

We have seen how the staminate disk of *Cycadeoidea ingens*, and of all the other species so far known, bears inside the campanula or androecium many functional synangia on the rachial axes, either inserted directly or on pinnules. Now we see, furthermore, that the campanula remains large in a form with greatly reduced fronds, while we may be sure that interiorly borne synangia are still present on the rachial axes, or at least may be in related forms, whether we can detect them or not. Whence it follows that a slight further continuance of the rachial reduction, so plainly under way, must result in a toothed campanula bearing interiorly on each axial or rachial line only a single pair of synangia and finally a single synangium and no more, just as diagrammatically shown in *fig. 3*. Such types we may call, because of the strictly convolvulaceous aspect, *archaeosolandrous*, arbitrarily dismissing for the present all mention of the central ovulate region to which we return below.

Now plainly, having thus by a series of entirely simple stages reached this archaeosolandrous form, which we confidently believe will be detected in the fossil condition, it is only a minor step to simpler types of pollen sacs, either borne in pairs or singly, and finally to elongations of the filaments suiting the requirements of such flowers as that of *fig. 4*, which is none other than a common morning glory.

In short, the successive members of the series of steps outlined are these, letting capitals represent the known, and small letters the hypothetical plants:

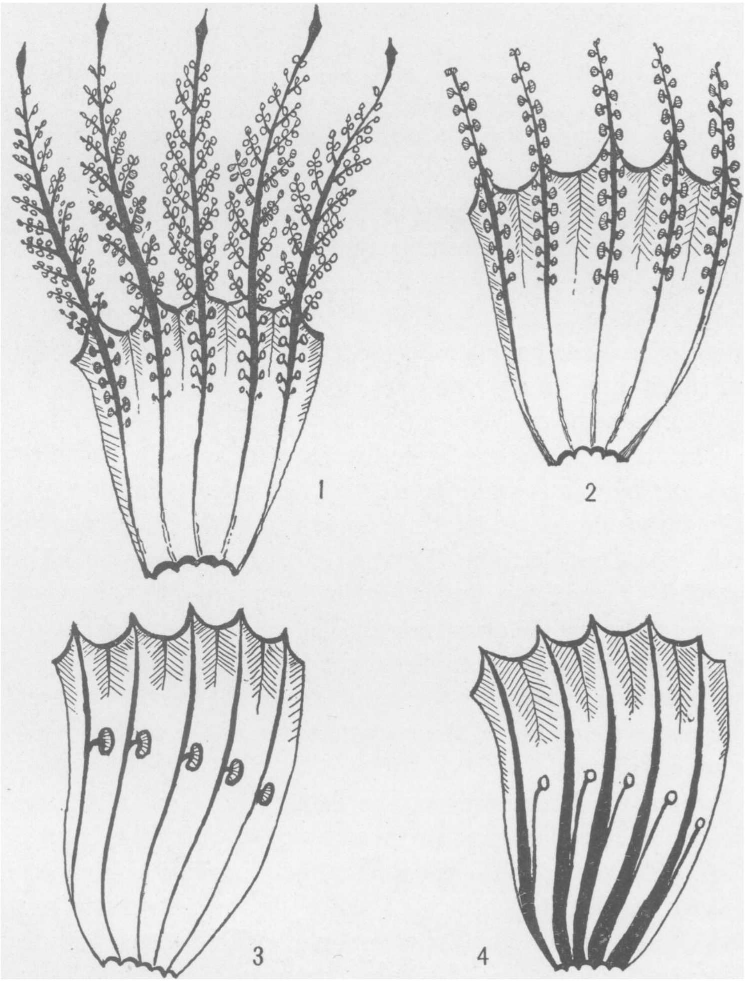
*A′*. Proangiosperms, or hemiangiosperms and pteridosperms.

*A*. The flower of *Cycadeoidea dacotensis*, with a campanulate disk of 18 bipinnate members.

*B*. The flower of *C. ingens*, with 12 bipinnate members.

*C.* The flower of *C. Jenneyana*, with only 10 bipinnate members, as well as various other greatly reduced and small types of flowers of Cycadeoidea.

*d.* A hypothetical flower of Cycadeoidea, with a staminate disk of 5 bipinnate members or staminate fronds (cf. *fig. 1*).



FIGS. 1–4

*E.* The El Consuelo staminate disk composed of 10 or 12 pinnate fronds.

*f.* A derivative of the El Consuelo disk, with only five pinnate fronds forming the campanula (cf. *fig. 2*).

*g.* A hypothetical campanula derived from the preceding by reduction of the synangial number to two and finally one, borne interiorly (*fig. 3*).

*h.* Unknown intervening plants derived from *g* and undergoing reduction in the number of the sporangial loculi, with thinning of the synangial wall, or

*i.* An unknown form much like *g*, but with a simpler type of pollinial organization. (This is the more probable member of the direct series, but both may be conceived of as having once existed.)

*j.* A campanula derived from either *h* or *i*, in which reduction to the angiospermous pollen sac has taken place, and in which elongation of the stamineal pedicels or filaments is going on (cf. *fig. 4*).

*K.* The staminate campanula of the convolvulaceous and many other gamopetalous flowers.

Thus may we derive the staminate zone of gamopetalous forms by a series of readily conceivable and closely united reduction stages, the principal members of which are in the larger sense already known. But let us now see if it be possible to go on and establish a plausible ovulate correlation; for if this cannot be done it is more than superfluous to say that *K* is in the extended sense not proven to be a true member of the evolutionary series *A′*, *A–j*.

That an apical series of spirally inserted carpophylls giving rise to a central ovulate cone played the chief rôle in the development of the Magnoliaceae, as in all the conifers and doubtless many other forms, is evident enough. But that such a cone was in *all* cases organized, or much less that a terminal group of diffuse carpophylls was present in all the ancestral phyla of the angiosperms, is after a little consideration seen to be a cumbrous hypothesis. By what other means then than by the reduction of the carpophylls and of cones may we conceive of the cognate origin of the ovulate region in angiosperms?

Perhaps the Draceneae may be made to give an initial answer. Take for instance the cultivated maguey (Agave) of Mexico, with its six immense versatile anthers borne on their long projecting filaments as seated in the interior surfaces of the six fused sporophylls, three of which are smaller, and the other three of which are alternately of larger size. On cutting this flower open and viewing it from the interior, is not the structure in reality that very diagrammatically indicated in *fig. 5*?

Now, was not this floral structure derived from a consolidating and changing whorl of six primitive bisporangiate fronds with basal megaspores and apical microspores? The simple method of derivation from such a primitive, or *archaeo-amarillidaceous* plant would consist in basi-lateral fusion of the sporophylls and development of a trilocular ovary, with the synchronous reduction and change of the microspore zone to the series of six interiorly borne stamens, after the manner shown to be feasible in the above series *A′*, *A–j*. Such we conceive to have been the origin of the yuccas and agaves; for it is no more improbable that heterospory should in many primitive stocks arise thus regularly in each of an apical whorl of sporophylls, than that it should find expression in the segregation of a basal group of megasporophylls followed by an apical group of microsporophylls, as in Cycadeoidea.

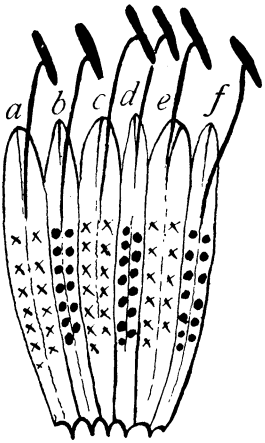


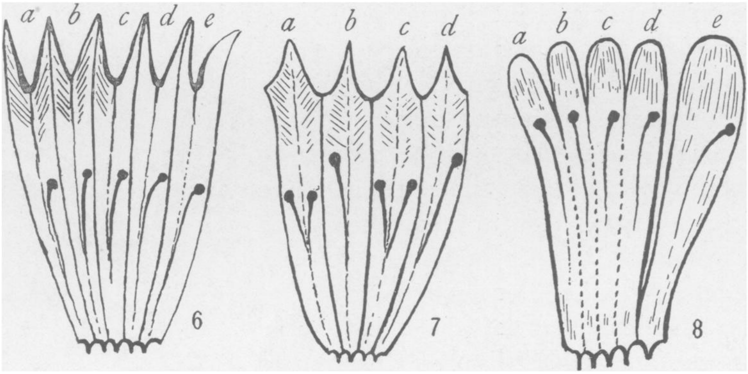
FIG. 5

Evidently in *Agave americana* the last stage of fusion resulted in the suppression of the basal or megaspore region of three alternate fronds. Nor is it so difficult to conceive how, the plant finding the inclosure of the ovarian region to its advantage, an elongation of the style finally resulted, with the retention of the gametophytes and seeds. Also, the long filaments must have been very readily produced by the flower under the stress of impulses that had to do with nothing else than the ordinary phenomena of fertilization. Such, surely, are the conclusions one may reach from the macroscopic examination of flowers like Agave and perchance likewise of the rose hip.

While the manner of evolution just outlined is in reality not utterly different from that of the Magnoliaceae, the order in which the parts are segregated clearly indicates a remote separation of the several stocks involved, and therefore the virtual polyphyletic origin of the angiosperms. But of course, when the initial changes, and when the major or crucial changes leading up to the two groups now considered so briefly, took place, and which group is in reality the more ancient, are questions that only the future may answer.

Having seen that the ovulate region, whether locular or strobilar, and whether there are few or many ovules, offers no impassable hiatus, it becomes desirable to interpret a few more examples of staminate organization leading toward or into the more complex types of flowers. Thus may we best test our theory and see if it applies to petals and stamens generally, and really affords a far-reaching explanation of floral constitution in the angiosperms, with ultimately a better basis of classification. But in so doing we may only take up a few forms; for an exhaustive analysis of the families based on the necessary histological and developmental data must be a truly gigantic task for many years and many workers.

Various gamopetalous flowers have the structure shown in *fig. 6*. Apparently the stamens alternate with the lobes of the corolla in such forms; but on closer examination it is seen that in reality the axis of the component leaves has shortened to form the notches. This difference, so convenient in classification, therefore rests on very slight anatomical distinction, unless it can be found to accompany a particular juxtaposition of the ovules throughout the groups in question. My example is from a shrub I found growing on the slopes of Popocatepetl, though anyone may turn to Gerardia and Pentstemon as equally good examples of this type of androecium.



FIGS. 6–8

Again, the cruciform flower invites attention, whether it be regarded as an approach toward or a departure from distinctly gamopetalous types. For in the cruciferous flower, although the stamen is apparently inserted on the common receptacle, rather than as in the diagrammatic *fig. 7*, there is considerable doubt if it is to be regarded as of discrete origin. Instead, it would seem more probable that although the point of stamineal attachment has become strongly depressed and indeed is virtually basal now, the flower has arisen very similarly to that shown in *fig. 4*. The two single stamens alternating with the two pairs thus form an opposing analogy to the suppression of megaspore regions in the Agave. But other explanations are also possible. For we believe that in the angiosperms petals have developed from bracts, that they have resulted from the complete sterilization of sporophylls, and that, as explained above, they result in vast numbers of instances from the apical expansion of a sporophyll, which, though greatly reduced, may still bear either megaspores or microspores or both.[3] And furthermore, we regard the stamens of Liriodendron as final reduction stages of individual sporophylls that were once large.

Of further interest in the cruciferous flower is the fact that little or no difference in the development of the petals accompanies the staminate change. But, on the contrary, in the diagram of a honeysuckle (*fig. 8*), while the stamens are of normal number and size,

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[3] There also appear to be various instances of more or less completely salver-shaped corollas, in which what are usually called the sepals are in reality fertile organs alternate with the petals, between which they press and fuse up to the beginning of the lobes of the corolla, and there bear stamens just as do the petals. Take for instance those forms with four "sepals," four petals, and eight stamens borne four on the petals and four alternately between them, but plainly scaling off with the members of the calyx. The cherry (*fig. 9* from GRAY) is perchance yet another example, but one retaining more stamens, these not being so distinctly determinate in number. (They may all be of the inner row.)

Perhaps as great a difficulty as we meet anywhere in applying these hypotheses of floral structure is in the case of a form like Silene with discrete hypogynous stamens and a free multiovulate ovary with an apparently distinct axial relation, for here there are several possibilities. Naturally that first coming to mind is that of a central carpellary whorl, followed below by a staminate whorl, and then by the members of the floral envelope. But another method needs to be reckoned with, namely, that which may be briefly characterized as a completed supero-axial shortening and consolidation of the bisporangiate fronds of an apical whorl, in such manner that basal megaspore-bearing pinnules assumed a vertical position and fused to form the ovary, style, and stigma, while the more apical microspore regions of these same fronds produced the stamens, the frond tips finally forming the corolla.

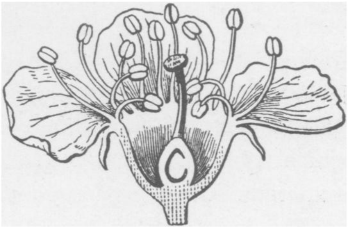

FIG. 9

the members of the corolla undergo division into a major and minor group. And plainly, from these simple phases we may no doubt ultimately pass by as simple steps and combinations to a reasonable interpretation of all the multifarious reductions, suppressions, and alterations in first one set of organs, and then another, resulting in papilionaceous, orchidaceous, and all the manifold forms of angiospermous flowers.

It is obviously not feasible adequately to show the derivation and the complex relations of sporophylls leading from the primitive to the higher types in any simple manner. Above all is this true because of the necessity of taking into account the varied possibilities and phases of monoecism and dioecism in any even approximately complete presentation. And the different rates of reduction at different periods, we are bound to assume, further complicate the problem. Indeed no one diagram and no one set of diagrams would serve to outline adequately the changes now suggested. Nevertheless, the attempt is made in *fig. 10* to give the simplest and most abbreviated expression of sporophyll change possible.

Have not the transformations really been easier than we think? Dictyozamites, the net-veined cycad, and many net-veined ferns of which some were doubtless seed-bearing, together with the forms of unknown fruit like Cissites, Vitiphyllum, and Liriodendropsis, all go to show that there is no special hiatus between the angiospermous foliage and the more primitive seed-bearing plants. A single new locality in the upper Triassic or lower Jurassic may at any time completely close the foliage gap. Again, the stem structure of the angiosperms presents no difficulty of derivation from the older types, in which free branching is already known, as well as the presence of numerous flowers undergoing great reductions and changes.

The great double funnels of the near-by Ipomoea, nearly a foot in length, show how readily fusions have gone on, and how great must have been the changes, reactions, and alterations going on for ages in all floral organs. The balance once disturbed, or a critical stage or plastic form once accomplished, infinite changes in a truly polyphyletic race set in.

Other fossil evidence for metamorphosis and reduction will be forthcoming, and speedily. But the student of fossils now realizes

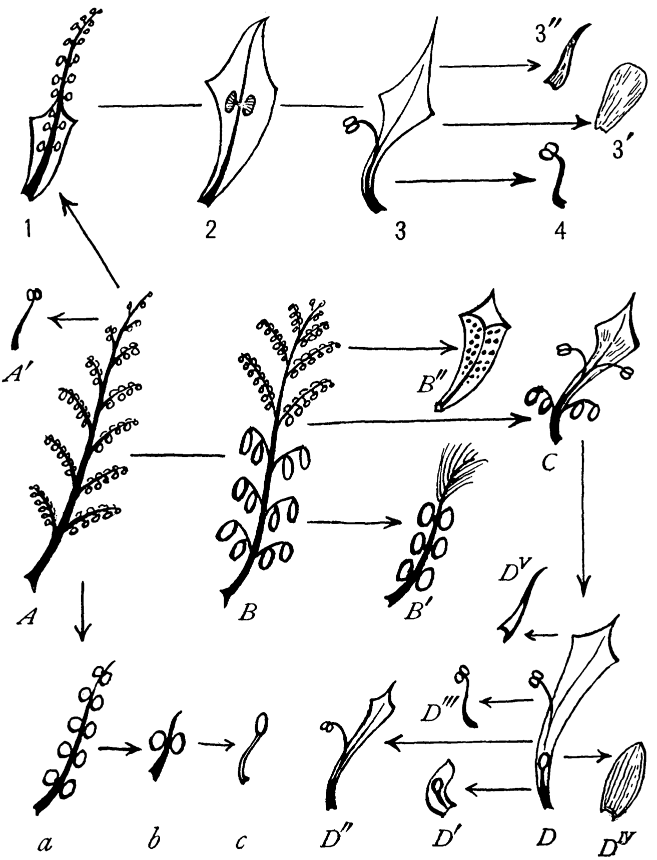

FIG. 10.—Theoretical and actual stages in the development of megasporophylls and microsporophylls of existing spermatophytes from hypothetical homosporous fronds.

*A*, homosporous early pteridophytes (Paleozoic); *B*, heterosporous pteridophyte derived from *A* (Permian ?).

$B'$, carpellary derivative of *B* (Permian; Cycas); $B''$, staminate derivative of *B* (Permian ?).

*C*, reduced form of *B* and a progenitor of gamopetalous angiosperms; *D*, further reduction stage of *C*, with potency of giving rise to all the essential organs and parts of a perfect flower; $D^{\prime-V}$, the stamino-petal ($D''$), carpel, stamen, petal, and sepal successively derived from *D*.

*a*, true carpellary leaf; *b*, reduced carpellary leaf; *c*, pedicellate ovule or seed (Cycadeoideae).

1, true staminate frond (Williamsonia, Cycadeoidea) of type leading to gamopetalous angiosperms; 2, true reduced staminate frond; 3, true stamino-petal; 4, stamen; $3'$, $3''$, second method of sepalo-petalous derivation.

GROUPS AND COMPLEXES.—$B'+B''$ (I–IV) = Cordaitales, Coniferales, Ginkgoales, Cycadales; $A+C$ (V) = Cycadeoideae and many proangiosperms; $A'+C$ (VI) = Magnoliaceae, Liriodendropsis, etc.; $A'+C$ (VII) = many types of naked flowers; $C+D$ (VIII) = gamopetalous and convolvulaceous forms; $D'+D''$ = many angiosperms; $A+a$ = proangiosperms.

that the proangiospermous or hemiangiospermous plant types which will exhibit critical developmental phases are likely to be inconspicuous, and that they must be studied with extreme care. Our hypothetical archaeosolandrous type, for instance, could be very easily missed, though found in excellent preservation. It will be necessary for that fortunate collector who finds the horizon and locality with lineal members of the early angiosperm line imbedded in it, to apply to his material all the newer laboratory methods, namely: (1) the staining, imbedding, and sectioning method used by Jeffrey and Hollick in dealing with forms apparently more like impressions or carbonaceous material than the partly preserved structures such as they finally found; (2) the developmental method, by means of which Beecher showed the preservation of the most delicate trilobite structures, and won such clear results; (3) the collodion method of Nathorst for recovering microscopic surface details, which are often present.

That intermediate types will be found in increasing number cannot be an idle prediction. That from time to time there will be found types definitely hypothesized, may be hopefully expected. Ten years ago I predicted the discovery of the seed ferns, now known in such number and variety. Even then it had become clear that "progressive prothallial elimination with correlated spore differentiation and alteration of the frondlike sporophytes of primitive ferns of the marattiaceous or an allied group were the basal factors in the evolution of the cycadofilicinean and cordaitean alliance." And it already seemed probable that the angiosperms could be added in this statement.

At the present time these groups seem to present more and more distinct points of contact, though in a very complex manner, apparently calling into requisition nearly every thinkable modification of the monosporangiate and bisporangiate frond, both on the same and on separate axes, and with nearly every conceivable variety of rearrangement, reduction, sterilization, and suppression. Even in the Cycadales, the better known of which form a really compact group, we have been compelled to say that the orders "do not appear to have passed through precisely the same evolutionary sequence of heterospory, bisporangiate or monosporangiate, monoecious, and finally doecious fructification."

And once more, we are compelled to hypothesize an extensive and far-reaching polyphyly for the angiosperms. But, none the less, the thought is also present that once an approach has been made along all the available lines of evidence, this seeming maze of possibilities may in the end be found vastly simpler than one can now picture. At least we are already persuaded that the day will come when the true relationships and derivation of every angiospermous family will be worked out and satisfactorily stated with mathematical precision.

El Instituto Geologico Nacional
de Mexico